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## The Smallest Snakefly (Raphidioptera: Mesoraphidiidae): A New Species in Cretaceous Amber from Myanmar, with a Catalog of Fossil Snakeflies

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## ABSTRACT

The world's smallest snakefly (Raphidioptera) is described and figured from a fossil preserved in Cretaceous amber from Myanmar (formerly Burma). *Nanoraphidia electroburmica*, new genus and species, is distinguished from other mesoraphidiids by characters of the wing venation and head morphology. Brief comments are made on the diminutive size of the specimen (forewing length just over 4 mm) and the geological history of the order is reviewed. Additionally, a larval snakefly is described from the same deposits, but is not considered to be congeneric with *Nanoraphidia*. A taxonomic catalog of all described, fossil snakeflies is appended. The following taxonomic changes are proposed: **Priscaenigmatidae**, new family, including *Priscaenigma* Whalley and *Hondelagia* Bode; Huaxiaraphidiidae, Sinoraphidiidae, and Jilinaraphidiidae, new synonyms of Mesoraphidiidae; *Cratoraphidia* and *Rudiraphidia*, new synonyms of *Baissoptera*; *Caloraphidia*, *Mioraphidia*, *Phiradia*, *Xynoraphidia*, and *Yanoraphidia*, new synonyms of *Mesoraphidia*; *Miofibla*, new synonym of *Fibla* (*Reisserella*); ***Creteroraphidiopsis***, new name for *Creteroraphidia* Willmann (non *Creteroraphidia* Ponomarenko); *Baissoptera pulchra* (Martins-Neto and Nel), new combination; *B. liaoningensis* Ren, resurrected combination; *Creteroraphidiopsis bontsaganensis* (Ponomarenko), new combination; *Fibla* (*Reisserella*) *cerdanica* (Nel), new combination; *Pararaphidia vitimica* (Martynova), new combination; *Mesoraphidia furcivenata* Ren and *M. pterostigmalis* Martynova, resurrected combinations; and *M. gaoi* (Ren), *M. glossophylla* (Ren), *M. longistigmata* (Ren), *M. myri-oneura* (Ren), *M. obliquivenatica* (Ren), *M. polyphlebia* (Ren), and *M. shangyuanensis* (Ren), all new combinations in *Mesoraphidia*.

## INTRODUCTION

Among the orders of holometabolous insects, a lineage renowned as the most diverse radiation of animal life, the snakeflies (Raphidioptera) comprise the least speciose group (ca. 206 modern species) and are among the most distinctive and remarkable of lineages. The order is readily recognizable for the elongate prothorax and long ovipositor in females, among other traits, although true autapomorphies for the group are not immediately evident. Today the order consists of approximately 206 species entirely restricted to the Northern Hemisphere and principally in temperate habitats at latitudes and altitudes that experience a cold winter (Aspöck, 1998; Aspöck, Aspöck, and Rausch, 1991, 1998, 1999a, 1999b; Aspöck, Aspöck, and Yang, 1998; Yang, 1998). A particular concentration of species can be found in Central Asia and around the Tien Shan Mountain range passing from Tadjikistan, through Kyrgyzstan, and extending into western Uzbekistan, southeastern Kazakhstan, and the northwestern borders of China (Aspöck et al., 1999a). Species of the order are arboreal. Larvae are generalist predators and relatively long-lived, principally living under the bark of trees and shrubs (a few raphidiids live in leaf litter at the base of

shrubs). Adults are short-lived and, like the larvae, are predaceous, although capable of capturing only weak prey. Species are generally inept flyers and thereby poor dispersers, making the group susceptible to vicariant events and subsequent adaptation and speciation.

Together with Neuroptera and Megaloptera the Raphidioptera comprise the superorder Neuropterida and the living adelphotaxon of the beetles (Coleoptera) (Mickoleit, 1973; Kristensen, 1991, 1999; Whiting et al., 1997; Hörschmeyer, 1998, Carpenter and Wheeler, 1999; Wheeler et al., 2001). While the overall position of the superorder within Holometabola is of little debate, some controversy remains concerning the relative positions among the three neuropterid orders. Most of the recent studies from both morphological and molecular evidence have converged to support a Raphidioptera + Megaloptera sister-group relationship (e.g., Whiting et al., 1997; Carpenter and Wheeler, 1999). This is somewhat supported by paleontological evidence since for the earliest of fossil snakeflies the hind wing venation is remarkably megalopteran-like while the forewings are typical for primitive Raphidioptera (see Discussion below and under Priscaenigmatidae in appendix 1), tantalizingly suggesting that the Raphidioptera are indeed more close-

ly allied to the Megaloptera and diverged from them in the early Mesozoic.

Fossils of snakeflies have been recognized since the middle of the 19th century. The first fossil was described as *Raphidia (Inocellia) erigena* Menge (Menge, 1856; Pictet-Baraban and Hagen, 1856) from an individual preserved as an amber inclusion from the Tertiary of northern Europe. Throughout the remainder of the 19th century and well into the early 20th century numerous other Tertiary snakeflies were described from compression fossils in North America, almost exclusively from Florissant, Colorado (appendix 1). In 1925 the great founder of Russian paleoentomology Martynov (1925a, 1925b) discovered the first Mesozoic representatives of the order in Upper Jurassic deposits of Central Asia. Subsequently, Carpenter (1967), Bode (1953), and Martynova (1947, 1961) proposed additional Jurassic and Cretaceous species adding significantly to our knowledge of the group. Modern authors have proposed numerous more Mesozoic species, principally from the Upper Jurassic and Cretaceous of Asia (e.g., Ponomarenko, 1993; Ren, 1997), but also from the Jurassic of Europe (Whalley, 1985; Willmann, 1994) and the Lower Cretaceous of Brazil (e.g., Oswald, 1990); all are preserved as compressions. Lower Cretaceous species are also known from Spain (Martínez-Delclòs, 1991; Peñalver et al., 1999) and Korea (Engel, unpubl. data), but remain undescribed. Although numerous Paleozoic species have been described as plesiomorphic lineages of Raphidioptera, all have subsequently been removed from the order (see Discussion, below).

Until recently, amber snakeflies were restricted to those preserved in middle Eocene (Lutetian) Baltic amber (Carpenter, 1956; Engel, 1995; Weitschat and Wichard, 1998). Grimaldi (2000) described the first Cretaceous-amber snakefly in Turonian amber from New Jersey—the first representative of the extinct family Mesoraphidiidae in amber—as well as a mesoraphidiid larva from the same deposits. Herein a second Cretaceous amber snakefly, also of the Mesoraphidiidae, is described and figured. The new species was discovered in Cretaceous (Cenomanian?) amber from Myanmar and is the

first Mesozoic amber snakefly from the Old World. The age and fauna of Burmese amber has most recently been considered by Zherikhin and Ross (2000) and Grimaldi et al. (2002), although several earlier authors have also presented accounts of its age (e.g., Cockerell, 1917). A raphidiopteran larva has also been recovered from these same deposits (Rasnitsyn and Ross, 2000; Engel, personal obs., see below), but is not conspecific with the imago described below and, although perhaps a mesoraphidiid, cannot be confidently assigned to family. Perhaps the most remarkable attribute of the adult specimen considered herein is its diminutive size. The forewing length of the individual is just under 4.5 mm making it the smallest snakefly, living or fossil. This new and particularly noteworthy species is described to make its name available for papers considering the paleontological significance of Burmese amber (Grimaldi et al., 2002) as well as a forthcoming monograph on the neuropterid fauna of Burmese amber (Engel, in prep.). In addition, an overview of the geological history of the order is presented with a taxonomic catalog of fossil snakeflies appended (appendix 1). Morphological terminology follows that of Aspöck et al. (1991).

## SYSTEMATIC PALEONTOLOGY

### *Nanoraphidia*, new genus

TYPE SPECIES: *Nanoraphidia electroburmica*, new species.

DIAGNOSIS: Minute size (forewing length under 5 mm, fig. 1). Head ovoid, gently tapering posterad posterior tangent of compound eyes (fig. 2; similar to heads of Raphidiidae); three large ocelli present, positioned near posterior tangent of compound eyes, posterior border of head without, shallow, collarlike lip; antenna inserted posterior to clypeal-frons suture, slightly basad anterior tangent of compound eyes; antenna longer than head; clypeus truncated, apical margin only slightly extending beyond anterior tangent of compound eyes; compound eyes large and exophthalmic; coronal suture absent. Pronotum subequal in length to head length, with anterior half narrowed dorsoventrally relative to posterior half (i.e., with slight downward curve in lateral view, see fig. 2).

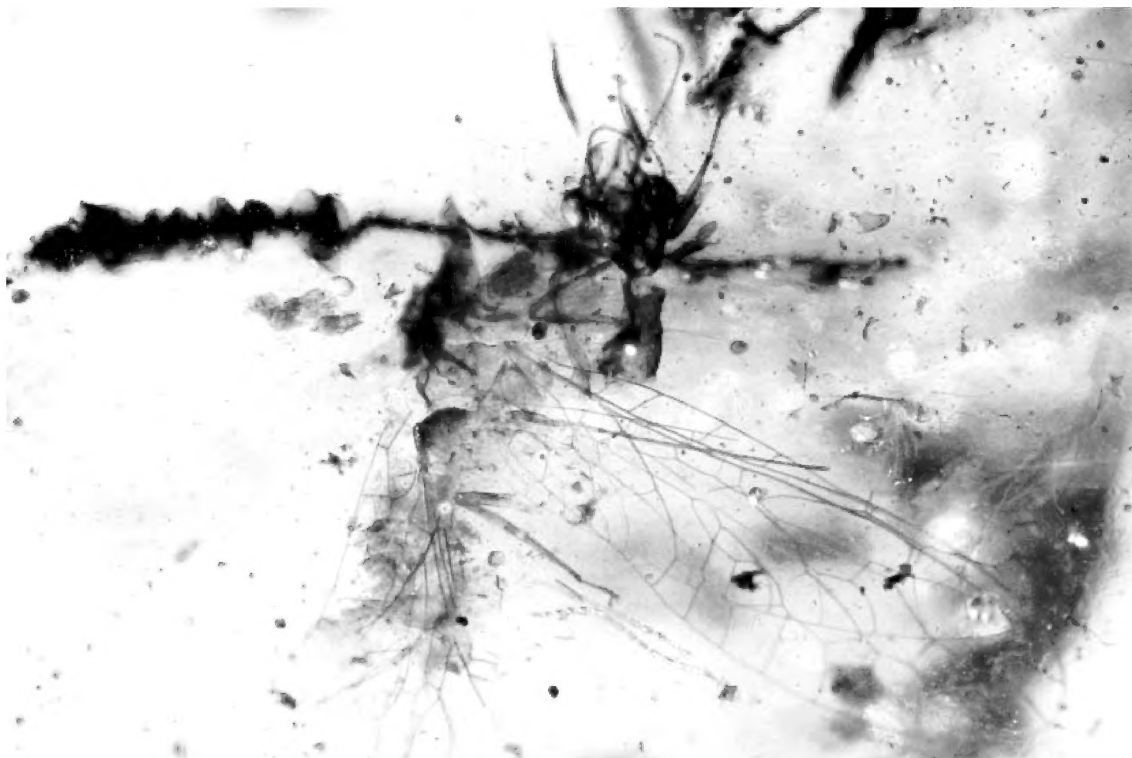


Fig. 1. Photomicrograph of holotype of *Nanoraphidia electroburmica*, new genus and species (AMNH Bu-092).

Forewing with costal area relatively broad, at widest point costal field 1.75 times broader than pterostigma (as broad or narrower than pterostigma in other Mesoraphidiidae); pterostigma elongate, without crossveins; Sc terminating into C near wing midpoint; single medial cell posterior to MP (2–3 medial cells posterior to MP in *Mesoraphidia*); first cuacup crossvein strongly basad M-CuA separation (at or separated by a few vein widths in other mesoraphidiids).

ETYMOLOGY: The new genus-group name is a combination of *nanos* (Greek, meaning “dwarf”) and *Raphidia*. The name is feminine.

COMMENTS: The expanded costal area is reminiscent of the same feature in *Cretinocellia* and *Lugala* (Ponomarenko, 1988; Willmann, 1994); however, both of these genera are baissopterids, exhibiting the rich crossveins and dense number of cells between Rs and M. The slightly expanded costal area is likewise similar to the living families Raphidiidae and Inocelliidae.

*Nanoraphidia electroburmica*,  
new species

Figures 1–3

DIAGNOSIS: As for the genus (see above).

DESCRIPTION: As for the genus with the following additions: Forewing length 4.26 mm. Integument dark brown, without maculations, faintly imbricate (where evident); wing veins brown, membrane hyaline, pterostigma faintly infumate. Mandible with large, curved, apical tooth separated from series of minute, median serrations by deep notch; compound eye length nearly as long as head posterad posterior tangent of compound eyes; compound eyes separated by distance slightly greater than compound eye length; inner margins of compound eyes relatively straight and parallel; 20 flagellomeres, each about as long as wide, with sparse, minute setae. Five tarsal segments, third bilobed; claws simple; arolium large. Forewing with pterostigma elongate (more so than in most other mesoraphidiids, fig. 3), but begin-

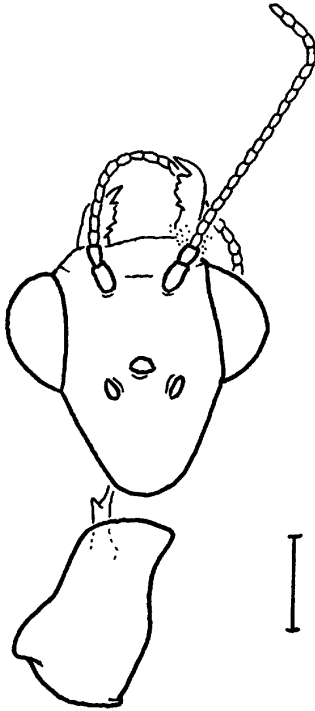


Fig. 2. Dorsal of head and dorsolateral oblique view for pronotum of holotype of *Nanoraphidia electroburmica*, new genus and species (AMNH Bu-092). Scale bar = 0.25 mm.

ning beyond termination of Sc, without transverse pterostigmal crossveins except at very base of pterostigma and distad terminus of Sc by 1.75 times pterostigmal width; pterostigma longer than either radial cell; veins meeting wing margins not apically bifurcate; five costal crossveins (c-sc); single, proximal sc-r crossvein; two large radial cells present, with two posterior cells immediately behind and progressively decreasing in size; first radial cell distinctly longer than second radial cell, with posterior radial branch arising slightly basad its midpoint; single medial cell present; M-CuA separation positioned near midpoint between two cua-cup crossveins; A2 strongly arcuate proximally; minute jugal lobe not evident (remaining venational details depicted in fig. 3). Preserved portion of hind wing as depicted in Figure 3. Thorax and abdomen largely crushed, but overall length can be determined from the remains

and abdominal apex does not surpass forewing apex.

HOLOTYPE: AMNH Bu-092; Myanmar (Burma), Upper Cretaceous [Cenomanian?], Kachin, Tanai Village, on Ledo Road 105 km NW Myitkyna, coll. Leeward Capitol Corp., 1999. Labeled "HOLOTYPE, *Nanoraphidia electroburmica* Engel". Deposited in the amber collection, Division of Invertebrate Zoology, AMNH. The individual of *Nanoraphidia* is preserved in a large piece of clear, orange-colored amber measuring approximately 1.8 cm wide, 2.0 cm long, and gently tapering on one end from a height of 1.3 cm down to 0.8 cm. The amber contains some internal flow-lines, but none of these obscure the snakefly. The amber was epoxy embedded following the procedure of Nascimbene and Silverstein (2000) prior to trimming, polishing, and eventual study with an Olympus stereomicroscope. In addition to the snakefly the amber also includes one spider, two mites, one thrips, six flies (three psychodids, one mycetophilid, one ceratopogonid, and one chironomid), one beetle, and one wasp. The body of the specimen is badly damaged, with much of the thorax and abdomen preserved as integumental debris. The pronotum, head, anterior legs, and wings are preserved nicely and somewhat cleared.

ETYMOLOGY: The specific epithet is a combination of *electrum* (Latin, meaning "amber") and Burma, former name of the country from which the amber originated.

#### Mesoraphidiid Larva

##### Figure 4

COMMENTS: This specimen is the oldest snakefly larva presently known. It is very likely neither conspecific nor congeneric with *N. electroburmica*, since the larva is several times larger than the adult described above. Aside from this specimen, there is only one other Cretaceous amber snakefly larva, preserved in Turonian amber from New Jersey (Grimaldi, 2000). Both specimens are perhaps mesoraphidiids. Additional immature snakeflies in amber are reported from the middle Eocene resins of the Baltic region (Weidner, 1958; Weitschat and Wichard, 1998).

Among immature Raphidioptera this spec-

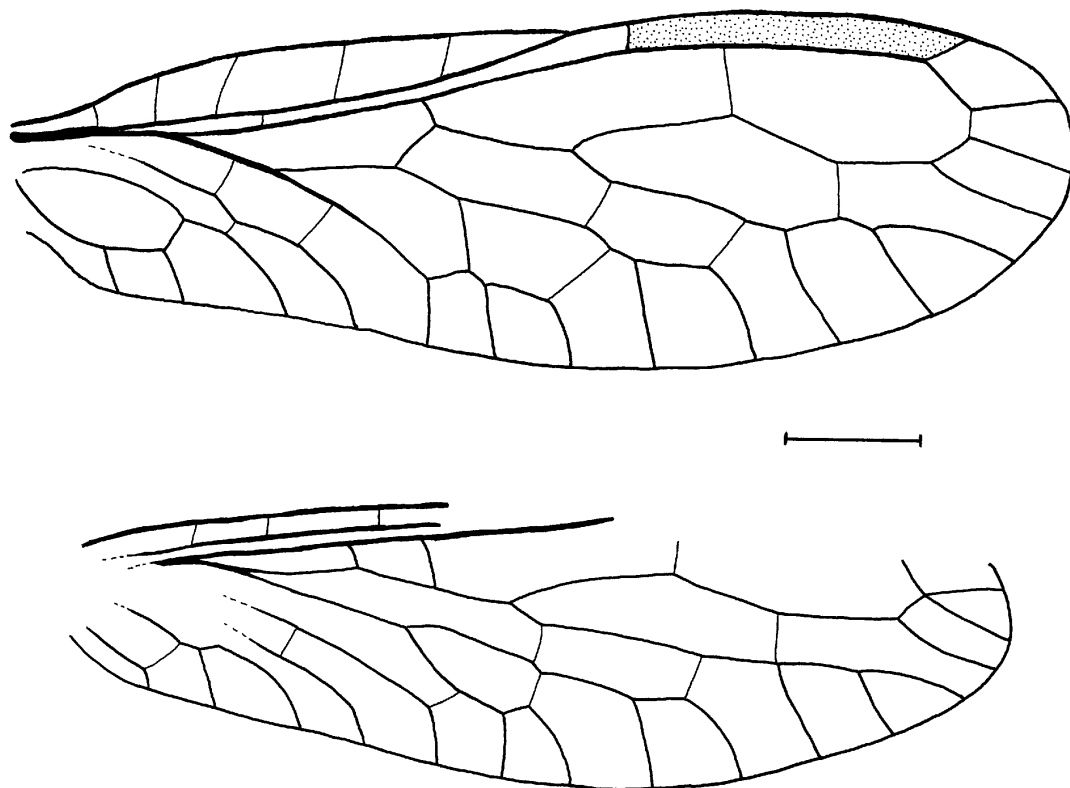


Fig. 3. Wing venation of *Nanoraphidia electroburmica*, new genus and species (AMNH Bu-092); forewing above, preserved portion of hind wing below. Scale bar = 0.5 mm.

imen is quite distinctive. The elongate and narrow head (fig. 4) is immediately diagnostic and quite different from other snakefly larva, fossil or extant (e.g., compare with those figured in Aspöck et al., 1991; Weitschat and Wichard, 1998; Grimaldi, 2000). The individual is nearly 14 mm in total length (easily much larger than *Nanoraphidia*) and the head alone is nearly 2 mm in length. Similarly, the three antennal segments are elongate and together slightly longer than the head. The prothorax is similarly elongate and the mesothorax slightly so; the metathorax and abdominal segments are more typical of modern snakeflies. Like the mesoraphidiid larva described by Grimaldi (2000), a distinct collar is not apparent as is for most Raphidiidae and Inocelliidae.

**MATERIAL:** Larva; Burmese amber, In. 20150 (BMNH). Preserved in a large slab of burmite with numerous other arthropod inclusions.

## DISCUSSION

To date all "cladistic" studies for Recent and fossil snakeflies have been greatly lacking and the higher phylogeny of the order is confused. The study by Ren and Hong (1994) based on an a priori polarization of six characters for seven terminals is not only the least rigorous but the most fraught with confusion surrounding characters (definitions and codings), identification of snakeflies, and basic systematic principles and theories. Characters from this study are quite dubious, some are clearly continuous without distinctions among states (e.g., prothorax short versus elongate, Rs originating just before or just after wing midpoint) or are based on homology statements that defy logic (e.g., "more crossveins" versus "less crossveins"). No characters were coded as polymorphic for particular lineages when indeed considerable variation exists within the ter-

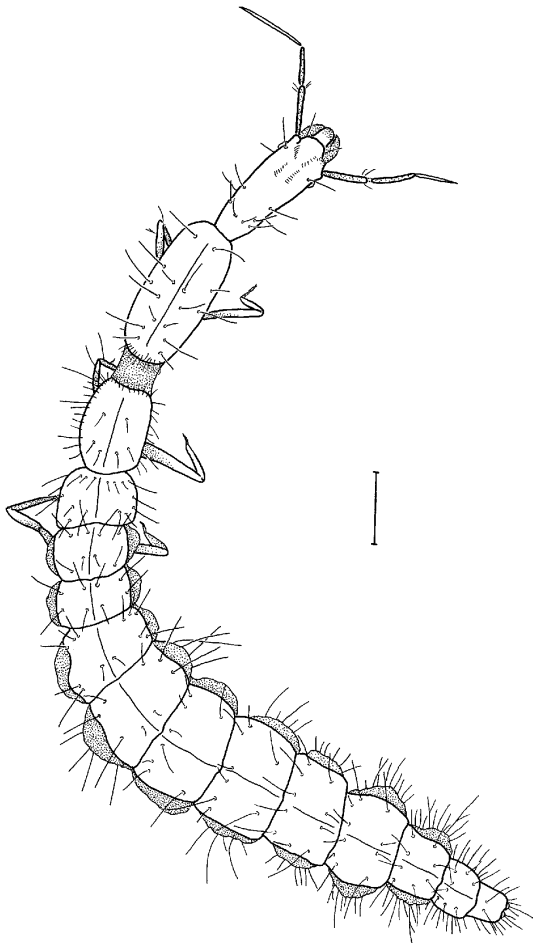


Fig. 4. Habitus of larval snakefly preserved in Burmese amber from the BMNH collection (In. 20150). Scale bar = 1.0 mm.

minals under consideration (e.g., Baissopteridae includes genera with and without pterostigmal veins and there is no clear picture as to which is the ground-plan state for the family, yet this terminal is coded as strictly present). Lastly, these authors claim to have demonstrated that the terminals in their analysis were monophyletic (in this instance, families) and yet, based on their own "data" and "analyses", two groups lack apomorphies altogether.

The study of Willmann (1994) was certainly more logically founded and more serious. Several familial exemplars were employed, thereby allowing for a more meaningful consideration of the monophyly of particular groups and the obviously errone-

ously assigned lineages removed. However, the definitions of several characters were similarly continuous and based on unnecessarily complicated transformation series, while some of the characters are simply tenuous. The homologies of particular veins may indeed be of some question, but the comparisons drawn by Willmann (1994) are no more sound than any presently employed. Despite these criticisms, Willmann (1994) has certainly prepared a stronger foundation for the incorporation of paleontological data in Raphidioptera phylogenetics than his predecessors. Although controversial, his hypotheses for relationships among snakeflies are more legitimately based and will require rigorous testing by future cladistic analyses in concert with a critical evaluation of homologies and a broader spectrum of character data. It is to be greatly regretted that the wealth of systematic data present in snakefly genitalia is not available for the fossil lineages.

As one might suspect, the classification of Mesozoic snakeflies is presently an inordinate mess and no clear picture of relationship presently exists. The "distinctive" features of several families are by no means unique to their supposed lineages and, in fact, numerous species are known to intermingle such attributes. The Jilinoraphidiidae and Huaxiraphidiidae are clearly synonyms of Mesoraphidiidae (these families are newly synonymized below; appendix 1). Similarly, although the Sinoraphidiidae is exceptionally poorly documented and described (Hong, 1982, 1992a, 1992b) it is certainly a synonym of Mesoraphidiidae (appendix 1). Despite the removal of these three Cretaceous "families", considerable confusion persists. The characters separating the remaining families (i.e., Baissopteridae, Mesoraphidiidae, and Alloraphidiidae) are poor. For instance, some of the "distinctive" traits defining the Alloraphidiidae from other families include the strongly distad position of MA relative to the origination of MP, the separation of CuA from M exceedingly close to the stem of R (nearly appearing as a trifurcation), reduced pterostigma, and the greatly elongate wings (Carpenter, 1967, 1992). The elongate wings are truly notable, but they are merely autapomorphic. The former two features are,



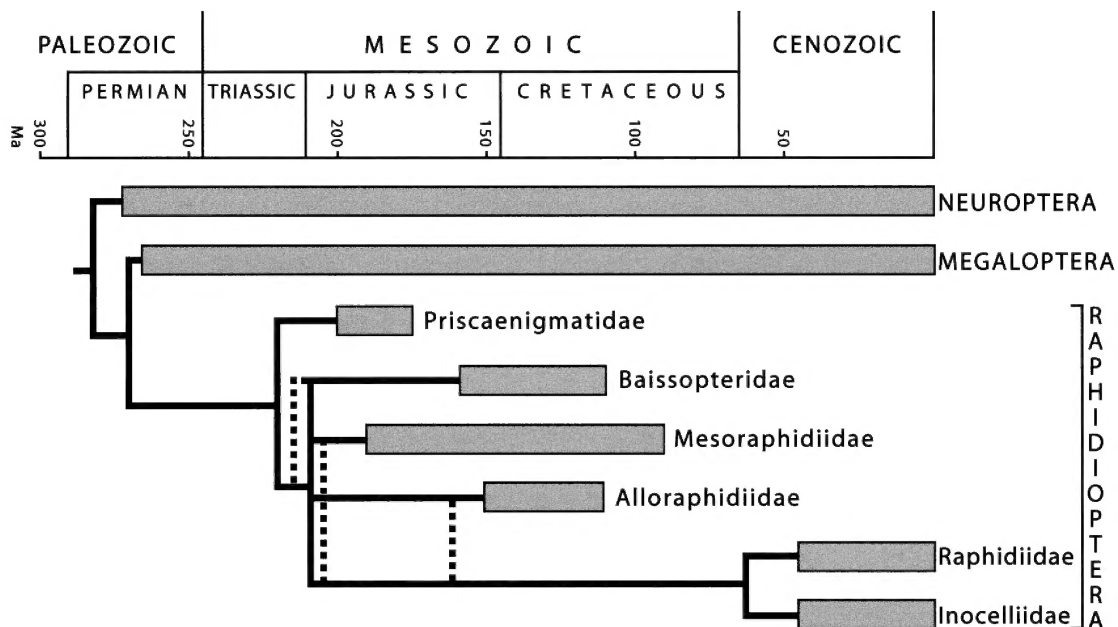


Fig. 5. Phylogeny of Raphidioptera. Broad, gray lines indicate known geological distributions; black lines are hypothesized ranges; dashed lines indicate alternative positions for particular groups and highlight the lack of a clear hierarchy of relationship. Characters are discussed in the text.

however, found in the living family Raphidiidae (e.g., some *Phaeostigma* species) as well as some mesoraphidiids, and for some of these traits there is continuous variation between the states resulting in a confusion concerning the homology of alternate states (i.e., it is difficult to consistently and confidently assign particular taxa to either character-state). Some genera that do appear on the surface to be valid (e.g., *Archeraphidia*, *Pararaphidia*) appear to further blend the boundaries of the families Alloraphidiidae and Mesoraphidiidae. The Baissopteridae appears to be more plesiomorphic than the Alloraphidiidae, Mesoraphidiidae, and extant families, assuming that the numerous cross-veins and cells are plesiomorphic. The Liassic genera *Priscaenigma* and *Hondelagia*, formerly classified in the Baissopteridae, represent a fundamentally different plan of wing venation and one that is plesiomorphic to all other snakeflies. In the forewing of Baissopteridae, Mesoraphidiidae, Alloraphidiidae, Raphidiidae, and Inocelliidae, the subcosta terminates into the costa near the midpoint of the wing. In both *Priscaenigma* and *Hondelagia* the subcosta extends to the wing

apex and appears to fuse directly with the radial system as in the Megaloptera (hind wings exhibit more typical raphidiopteran venation, e.g., see figures in Willmann, 1994). For this reason, both genera are here placed in a separate family, *Priscaenigmatidae* (appendix 1), and sister to all other Raphidioptera (fig. 5). The families of Recent and fossil snakeflies are summarized in table 1 while a hypothesis of their relationships and geological distribution is presented in Figure 5.

While the Raphidioptera are undoubtedly ancient, evidence of their occurrence in the Paleozoic has completely eroded (Carpenter, 1967, 1992; Sharov, 1968, 1971; Storozhenko, 1998; Storozhenko and Novokshonov, 1995; Shcherbakov, 1995), leaving the oldest definitive snakeflies as those from the Lower Jurassic. All Paleozoic families of snakeflies (i.e., Fatjanopteridae, Letopalopteridae, Permioraphidiidae, and Sojanoraphidiidae) have recently been removed from the order (although their assignment to Raphidioptera has been suspect for considerable time, e.g., Carpenter, 1967). The Permioraphidiidae, Sojanoraphidiidae, and Letopalopteridae were



TABLE 1  
Families of Raphidioptera and their Geological Distribution

Order RAPHIDOPTERA Navás <sup>a</sup>	
Suborder Priscaenigmatomorpha, new	
Family Priscaenigmatidae Engel, new	Lower Jurassic
Suborder Raphidiomorpha, new	
Family Baissopteridae Martynova	Uppermost Jurassic–Lower/Middle Cretaceous
Family Mesoraphidiidae Martynov	Lower Jurassic–Upper Cretaceous
Family Alloraphidiidae Carpenter	Lower-Middle Cretaceous
Family Raphidiidae Latreille	Eocene–Holocene
Family Inocelliidae Navás	Eocene–Holocene

<sup>a</sup>Navás (1916), following Shipley's (1904) mandate for a common *-ptera* suffix for insect ordinal names, was the first to use the ordinal name in this form and I have therefore attributed authorship to him even though earlier authors had also considered the snakeflies as a distinct order (under names such as Raphidiodea or other variants).

transferred to the orders Orthoptera (Carpenter, 1967, 1992; Sharov, 1968, 1971), Grylloblattaria (Storozhenko and Novokshonov, 1995), and Protorthoptera (Rasnitsyn *in* Novokshonov, 1998a, 1998b), respectively. The “ovipositor” of letopalopterids, in particular, was subsequently discovered to be preserved portions of legs, rather than a terminal structure (Novokshonov, 1998a, 1998b). Lastly, the family Fatjanopteridae was synonymized with the family Ampelipteridae in the Protorthoptera (Shcherbakov, 1995). While I agree that these families are not snakeflies, it must be noted that assignments to orders such as Orthoptera, Grylloblattaria, and Protorthoptera are equally questionable. Particularly dubious are the numerous Paleozoic and Mesozoic winged fossils assigned to Grylloblattaria (today an enigmatic and apterous order); none of these fossils preserve a single diagnostic synapomorphy of Grylloblattaria or even appear to share gross similarities (apomorphic or not) with modern grylloblattids, and thus the conjectures of diversity changes for this lineage (e.g., Storozhenko, 1998; Vršanský *et al.*, 2001) should be considered with serious skepticism. For Paleozoic and Mesozoic fossils the name Grylloblattaria has essentially become a meaningless, receptacle taxon for a polyphyletic assemblage of genera.

Although plesiomorphic with respect to the extant Raphidiidae and Inocelliidae, the earliest snakeflies from the Upper Jurassic already possessed the remarkable synapomorphies for the order. The Raphidioptera, therefore, likely extends well into the Triassic and

perhaps even the latest Permian. Although no direct evidence currently supports the conjecture that Raphidioptera is of Paleozoic origin, indirect evidence from the apparent geological ages of related clades (i.e., Neuroptera and Megaloptera) implies that the snakeflies are at least from the Late Triassic and perhaps as old as the Upper Permian (although this latter date is far less likely). Continued paleontological work will undoubtedly refine these estimates as more material becomes available from Triassic deposits. Based on currently available evidence, the snakeflies likely originated and diversified in the earliest Mesozoic after the cataclysmic Permian extinction event.

While modern snakeflies are not found in humid, tropical environments, it is clear that such habitat restrictions have not always been a characteristic of the order. The Cenomanian forests responsible for producing the Burmese amber in which *Nanoraphidia* occurred were perhaps the most tropical of all the Cretaceous amber localities (Grimaldi *et al.*, 2002). This is also true, although to a much lesser degree, of the amber-producing forests of the Middle Eocene in northern Europe where snakeflies are also known to have occurred (Carpenter, 1956; Engel, 1995; Weitschat und Wichard, 1998). Thus, tropical or subtropical snakeflies persisted at least into the early Tertiary but were perhaps relict and eventually extinguished by the climatic changes marking the Eocene-Oligocene transition. It is also abundantly clear that the order was globally distributed in the past (e.g., species from the Lower Cretaceous of South

America) and has undergone significant extinction. The broader distribution and climatic range of extinct snakefly lineages are likely linked. Overall the Cretaceous was much warmer than the Cenozoic (particularly so following precipitous drops in the Paleogene) and climatic changes perhaps drove many Raphidioptera lineages near extinction. As hypothesized by Aspöck (1998, 2000) the decline of the order was perhaps accentuated by the extraterrestrial impact and concomitant climatic disruption at the close of the Cretaceous. Those snakefly lineages not already adapted for colder climates in the early Tertiary would have been quickly extinguished. Extinction left the colder-adapted lineage of the Raphidiidae and Inocelliidae free to diversify in the temperate habitats of the Northern Hemisphere during the latest Paleogene and Neogene, thereby giving us the present distribution of the order.

#### ACKNOWLEDGMENTS

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## APPENDIX 1

### TAXONOMIC CATALOG OF FOSSIL SNAKEFLIES (RAPHIDIOPTERA)

The following preliminary catalog attempts to summarize the named fossil species of snakeflies. Undescribed or unnamed fossils are not included as are subsequent references (except for those that make taxonomic changes, e.g., new combinations, synonymies, nomina nova). Taxonomic summaries are provided for all species and for all extinct higher taxa. Names in quotation marks are those believed to be dubiously assigned as to genus; e.g., owing to the absence of information on genitalic characters fossil species presumed to be of *Raphidia* cannot be confidently placed in this genus. The names *Archiiinocellia* and *Arariperaphidia* are listed as incertae sedis. Names are in alphabetical order; refer to Table 1 in the text for an indication of the geological range of each family. A dagger (†) indicates an extinct taxon. A revised, phylogenetic classification of fossil snakeflies is presently in progress and will hopefully further clarify affinities of the species outlined below (Engel, in prep.).

A plethora of ill-defined snakefly families, genera, and species from Central and Eastern Asia has been cavalierly proposed (e.g., Hong, 1982, 1992a, 1992b, 1992c; Hong and Chang, 1989; Ponomarenko, 1988, 1993; Ren, 1994, 1997; Ren et al., 1995). Many of these taxa are founded on one or two minute characters (e.g., the presence or absence of a single crossvein!) and upon characters that are either not diagnostic (i.e., occur in other families) or rampantly variable among species within well-founded genera or even within a single species! Furthermore, several of these genera seem to have been randomly assigned to families without a careful consideration of the character basis for doing so. Several of these genera simply lack all defining features of the particular family in which they were originally placed, while exhibiting all of the characters of another family (and frequently of a previously proposed genus!). In instances where the position of a given group or species is clear I have proposed a transfer, new combination, and/or synonymy. It must be noted, however, that this "housekeeping" is merely preliminary and more detailed work will be required. Certainly several of the Asian species will prove to be synonyms, but I have tentatively retained them as valid species herein.

The following taxonomic changes are proposed herein: **New taxa:** *Pricaeenigmatomorpha*, new suborder; *Priscaenigmatidae*, new family for *Priscaenigma* and *Hondelagia*; and *Cretoraphidiopsis*, new name for *Cretoraphidia* Willmann (non Ponomarenko). **New synonymies:** *Huaxiaraphidiidae*, *Sinoraphidiidae*, and *Jilinoraphidiidae*, new synonyms of *Mesoraphidiidae*; *Cratoraphidia* and *Rudiraphidia*, new synonyms of *Baissoptera*; *Miofibla*, new synonym of *Fibla* (*Reisserella*); *Caloraphidia*, *Mioraphidia*, *Phiradia*, *Xynoraphidia*, and *Yanoraphidia*, new synonyms of *Mesoraphidia*. **New combinations:** *Baissoptera pulchra* (Martins-Neto and Nel), *Cretoraphidiopsis bontsaganensis* (Ponomarenko), *Fibla* (*Reisserella*) *cerdanica* (Nel), *Mesoraphidia gaoi* (Ren), *M. glossophylla* (Ren), *M. longistigmosa* (Ren), *M. myrioneura* (Ren), *M. obliquivenatica* (Ren), *M. polyphlebia* (Ren), *M. shangyuanensis* (Ren), and *Pararaphidia vitimica* (Martynova). **Resurrected combinations:** *Baissoptera liaoningensis* Ren, *Mesoraphidia furcivenata* Ren, and *M. pterostigmalis* Martynova.

#### ORDER RAPHIIDOPTERA NAVÁS

##### Family †ALLORAPHIDIIDAE Carpenter

†Alloraphidiidae Carpenter, 1967 [1968]: 270.  
Type genus: †*Alloraphidia* Carpenter, 1967.

##### Genus †*Alloraphidia* Carpenter

†*Alloraphidia* Carpenter, 1967 [1968]: 270. Type species: †*Alloraphidia dorfi* Carpenter, 1967, monobasic and original designation.

##### †*Alloraphidia anomala* Ren

†*Alloraphidia anomala* Ren, 1997: 181. Lower Cretaceous, Beipiao, Liaoning, China.

##### †*Alloraphidia asiatica* Ponomarenko

†*Alloraphidia asiatica* Ponomarenko, 1993: 75. Upper Jurassic–Lower Cretaceous, Baisa, Buryat, Russia.

##### †*Alloraphidia dorfi* Carpenter

†*Alloraphidia dorfi* Carpenter, 1967 [1968]: 271. Middle Cretaceous, Labrador, Canada.

##### †*Alloraphidia petrosa* Ponomarenko

†*Alloraphidia petrosa* Ponomarenko, 1988: 80. Lower Cretaceous, Mongolia.

##### Genus †*Archeraphidia* Ponomarenko

†*Archeraphidia* Ponomarenko, 1988: 78. Type species: †*Archeraphidia yakowlewi* Ponomarenko, 1988, original designation.

##### †*Archeraphidia baisensis* Ponomarenko

†*Archeraphidia baisensis* Ponomarenko, 1993: 79. Upper Jurassic–Lower Cretaceous, Baisa, Buryat, Russia.

##### †*Archeraphidia hosbayari* Ponomarenko

†*Archeraphidia hosbayari* Ponomarenko, 1988: 79. Lower Cretaceous, Mongolia.

##### †*Archeraphidia yakowlewi* Ponomarenko

†*Archeraphidia yakowlewi* Ponomarenko, 1988: 78. Lower Cretaceous, Mongolia.

##### Genus †*Pararaphidia* Willmann

†*Pararaphidia* Willmann, 1994: 178. Type species: †*Alloraphidia deserta* Ponomarenko, 1988, monobasic and original designation.

COMMENTS: This genus is particularly noteworthy for blurring the distinctions between *Mesoraphidiidae* and *Alloraphidiidae*. It is placed here

with hesitation. Willmann (1994: 180) stated that there were two species of *Pararaphidia*, but did not identify the second species. Herein I identify a second species, *Pararaphidia vitimica* (Martynova), but it is apparently not the one Willmann had in mind since he presumably considered *Pro-raphidia* to contain the two species originally placed there by Martynova (1947, 1961).

†*Pararaphidia deserta* (Ponomarenko)

†*Alloraphidia deserta* Ponomarenko, 1988: 79. Lower Cretaceous, Mongolia.

†*Pararaphidia deserta* (Ponomarenko); Willmann, 1994: 178.

†*Pararaphidia vitimica* (Martynova),  
new combination

†*Proraphidia vitimica* Martynova, 1961: 82. Upper Jurassic–Lower Cretaceous, Baisa, Buryat, Russia.

†*Alloraphidia vitimica* (Martynova); Ponomarenko, 1993: 78.

Family †BAISSOPTERIDAE Martynova

†Baissopteridae Martynova, 1961: 80. Type genus: †*Baissoptera* Martynova, 1961.

†Baissopteridae Hong, 1989: 293. *Lapsus calami*.

Genus †*Austroraphidia* Willmann

†*Austroraphidia* Willmann, 1994: 177. Type species: †*Raphidia brasiliensis* Nel, Séméria, and Martins-Neto, 1990, monobasic and original designation.

COMMENTS: This genus is perhaps best considered a junior subjective synonym of *Baissoptera*; however, the distal position of MA relative to the origination of MP in the forewing, the slightly fewer number of cells in the posterior half of the wing, and the exceptionally short M+ CuA in the hind wing (i.e., M and CuA separate almost immediately distad divergence from stem of R) suggests that this species is indeed generically distinct.

†*Austroraphidia brasiliensis*  
(Nel, Séméria, and Martins-Neto)

†*Raphidia brasiliensis* Nel, Séméria, and Martins-Neto, 1990: 29. Lower Cretaceous, Ceará, Brazil.

†*Austroraphidia brasiliensis* (Nel, Séméria, and Martins-Neto); Willmann, 1994: 177.

Genus †*Baissoptera* Martynova

[Upper Jurassic, Lower Cretaceous]

†*Baissoptera* Martynova, 1961: 80. Type species: †*Baissoptera martinsoni* Martynova, 1961, original designation.

†*Cratoraphidia* Martins-Neto and Nel, 1992: 426. Type species: †*Cratoraphidia pulchra* Martins-Neto and Nel, 1992, monobasic and original designation. NEW SYNONYMY.

†*Rudiraphidia* Ren, 1997: 175. Type species: †*Baissoptera liaoningensis* Ren, 1994, monobasic and original designation. NEW SYNONYMY.

COMMENTS: Both genera differ only in features that are known to be variable among living species and therefore poor characters upon which to establish new genera. There is no truly diagnostic character upon which to distinguish these groups and they are therefore synonymized here.

†*Baissoptera brasiliensis* Oswald

†*Baissoptera brasiliensis* Oswald, 1990: 154. Lower Cretaceous, Ceará, Brazil.

†*Baissoptera cellulosa* Ponomarenko

†*Baissoptera cellulosa* Ponomarenko, 1993: 64. Upper Jurassic–Lower Cretaceous, Baisa, Buryat, Russia.

†*Baissoptera elongata* Ponomarenko

†*Baissoptera elongata* Ponomarenko, 1993: 66. Upper Jurassic–Lower Cretaceous, Baisa, Buryat, Russia.

†*Baissoptera euneura* Ren

†*Baissoptera euneura* Ren, 1997: 173. Lower Cretaceous, Beipiao, Liaoning, China.

†*Baissoptera grandis* Ren

†*Baissoptera grandis* Ren in Ren et al., 1995: 97. Lower Cretaceous, Beipiao, Liaoning, China.

†*Baissoptera liaoningensis* Ren,  
resurrected combination

†*Baissoptera liaoningensis* Ren, 1994: 132. Lower Cretaceous, Beipiao, Liaoning, China.

†*Rudiraphidia liaoningensis* (Ren); 1997: 176.

†*Baissoptera martinsoni* Martynova

†*Baissoptera martinsoni* Martynova, 1961: 80. Upper Jurassic–Lower Cretaceous, Baisa, Buryat, Russia.



†*Baissoptera kolosnitsynae* Martyonva, 1961: 81.  
Upper Jurassic–Lower Cretaceous, Baisa, Buryat, Russia.

†*Baissoptera minima* Ponomarenko

†*Baissoptera minima* Ponomarenko, 1993: 63.  
Upper Jurassic–Lower Cretaceous, Baisa, Buryat, Russia.

†*Baissoptera pulchra* (Martins-Neto and Nel),  
new combination

†*Cratoraphidia pulchra* Martins-Neto and Nel,  
1992: 427. Lower Cretaceous, Ceará, Brazil.

†*Baissoptera sibirica* Ponomarenko

†*Baissoptera sibirica* Ponomarenko, 1993: 66.  
Upper Jurassic–Lower Cretaceous, Baisa, Buryat, Russia.

Genus †*Cretinocellia* Ponomarenko

†*Cretinocellia* Ponomarenko, 1988: 74. Type species: †*Cretinocellia cellulosa* Ponomarenko, 1988, original designation.

†*Cretinocellia cellulosa* Ponomarenko

†*Cretinocellia cellulosa* Ponomarenko, 1988: 76.  
Lower Cretaceous, Mongolia.

Genus †*Creteraphidia* Ponomarenko

†*Creteraphidia* Ponomarenko, 1993: 68. Type species: †*Creteraphidia certa* Ponomarenko, 1993, original designation.

†*Creteraphidia certa* Ponomarenko

†*Creteraphidia certa* Ponomarenko, 1993: 68.  
Upper Jurassic–Lower Cretaceous, Baisa, Buryat, Russia.

†*Creteraphidia macrocella* Ponomarenko

†*Creteraphidia macrocella* Ponomarenko, 1993: 69.  
Upper Jurassic–Lower Cretaceous, Baisa, Buryat, Russia.

†*Creteraphidia magna* Ponomarenko

†*Creteraphidia magna* Ponomarenko, 1993: 71.  
Upper Jurassic–Lower Cretaceous, Baisa, Buryat, Russia.

†*Creteraphidia reticulata* Ponomarenko

†*Creteraphidia reticulata* Ponomarenko, 1993: 69.  
Upper Jurassic–Lower Cretaceous, Baisa, Buryat, Russia.

†*Creteraphidiopsis*, nomen novum

†*Creteraphidia* Willmann, 1994: 176. Type species: †*Cretinocellia bontsaganensis* Ponomarenko, 1988, monobasic and original designation. *Nomen praeoccupatum* (nec †*Creteraphidia* Ponomarenko, 1993).

ETYMOLOGY: The new genus-group name is a combination of the original name *Creteraphidia* and the suffix *-opsis* (meaning “looking like”). The name is feminine.

†*Creteraphidiopsis bontsaganensis* (Ponomarenko), new combination

†*Cretinocellia bontsaganensis* Ponomarenko, 1988: 76. Lower Cretaceous, Mongolia.

†*Creteraphidia bontsaganensis* (Ponomarenko); Willmann, 1994: 176.

Genus †*Lugala* Willmann

†*Lugala* Willmann, 1994: 176. Type species: †*Baissoptera longissima* Ponomarenko, 1988, monobasic and original designation.

†*Lugala longissima* (Ponomarenko)

†*Baissoptera longissima* Ponomarenko, 1988: 74.  
Lower Cretaceous, Mongolia.

†*Lugala longissima* (Ponomarenko); Willmann, 1994: 176.

Family INOCELLIIDAE Navás

Genus †*Electrinocellia* Engel

†*Electrinocellia* Engel, 1995: 192. Type species: †*Inocellia peculiaris* Carpenter, 1956, monobasic and original designation.

†*Electrinocellia peculiaris* (Carpenter)

†*Inocellia peculiaris* Carpenter, 1956: 80. Middle Eocene (Lutetian), Baltic amber.

†*Electrinocellia peculiaris* (Carpenter); Engel, 1995: 192.

Genus *Fibla* Navás

*Fibla* Navás, 1915a: 477. Type species: *Fibla hesperica* Navás, 1915a, monobasic and original designation.

*Burcha* Navás, 1915a: 478. Type species: *Inocellia maclachlani* Albarda, 1891, monobasic and original designation.

*Estoca* Navás, 1919: 91. Type species: *Estoca peyerimhoffi* Navás, 1919, monobasic.

*Inocellia* (*Reisserella*) H. Aspöck and U. Aspöck, 1971: 271. Type species: *Inocellia* (*Reisserella*) *pasiphae* H. Aspöck and U. Aspöck, 1971, monobasic and original designation.

†*Miofibla* Nel, 1993: 105. Type species: †*Miofibla cerdanica* Nel, 1993, monobasic and original designation. NEW SYNONYMY.

COMMENTS: *Miofibla* does not differ significantly from *Fibla* sensu lato and possesses the distinctive feature of five medial cells beyond MP in the forewing that is indicative of the subgenus *Reisserella*. I have therefore considered *Miofibla* synonymous with *Fibla* (and the subgenus *Reisserella* in particular).

†*Fibla* (*Fibla*) *carpenteri* Engel

†*Fibla* (*Fibla*) *carpenteri* Engel, 1995: 188. Middle Eocene (Lutetian), Baltic amber.

†*Fibla* (*Reisserella*) *cerdanica* (Nel),  
new combination

†*Miofibla cerdanica* Nel, 1993: 105. Upper Miocene, Bellver-en-Cerdaña, Spain.

†“*Fibla*” *erigena* (Menge)

†*Raphidia erigena* Menge, 1856: 15. *Nomen nudum*.

†*Raphidia* (*Inocellia*) *erigena* Menge In Pictet-Baraban and Hagen, 1856: 83. Middle Eocene (Lutetian), Baltic amber.

†*Inocellia erigena* (Menge); Scudder, 1890: 155.

†*Inocellia eogena* Scudder, 1890: 156. *Lapsus calami*.

†*Fibla erigena* (Menge); Carpenter, 1956: 79.

COMMENTS: Authorship of this species is often attributed to Hagen (e.g., Scudder, 1890; Carpenter, 1956; Oswald, 1990). Although the name was indeed first made available in the work of Pictet-Baraban and Hagen (1856), these authors clearly indicate those taxa that they propose as new and attribute to themselves while explicitly indicating respective authorship of other taxa. According to ICZN (1999: Art. 50.1.1) when explicit authorship is given to an individual other than the authors of the work, then authorship is to be attributed to that alternative person (in the present instance, to Menge).

†“*Fibla*” *exusta* (Cockerell and Custer)

†*Inocellia exusta* Cockerell and Custer, 1925: 295. Eocene-Oligocene boundary, Florissant, Colorado.

†*Fibla exusta* (Cockerell and Custer); Carpenter, 1936: 152.

#### Family †MESORAPHIDIIDAE Martynov

†Mesoraphidiidae Martynov, 1925a: 235. Type genus: †*Mesoraphidia* Martynov, 1925a.

†Sinoraphidiidae Hong, 1982: 152. Type genus: †*Sinoraphidia* Hong, 1982. NEW SYNONYMY.

†Jilinaraphidiidae Hong and Chang, 1989: 291. Type genus: †*Jilinaraphidia* Hong and Chang, 1989. NEW SYNONYMY.

†Huaxiaraphidiidae Hong, 1992a: 101. Type genus: †*Huaxiaraphidia* Hong, 1992a. NEW SYNONYMY.

†Mesoraphidae Hong, 1992c: 3. *Lapsus calami*.

COMMENTS: The status of Sinoraphidiidae was discussed in the text (see above) and justification for its synonymy is not repeated here. The family Jilinaraphidiidae was based on an incompletely preserved specimen (as indicated by Hong and Chang's figures) and the principal apomorphy that would perhaps justify its status is, in fact, an artifact of preservation. The absence of crossveins (and therefore cells in the forewing) would appear to be a remarkable apomorphy for the group. However, Hong and Chang's figures show a specimen with incompletely preserved venation (e.g., several of the longitudinal veins are not preserved over their length and are interrupted at many points). Some crossveins between branches of R are faintly preserved, but others are not. Since crossveins and the pterostigma are less sclerotized or pigmented than longitudinal veins, it is not surprising that in a specimen in which the stronger (i.e., longitudinal) veins are not entirely preserved, the crossveins in the same areas would be similarly missing. Until newer material of *Jilinaraphidia* is discovered and the absence of such venation authoritatively demonstrated, the justification for Jilinaraphidiidae is entirely unfounded. The genus appears, based on the limited evidence, to be a valid one within the Mesoraphidiidae.

#### Genus †*Baisoraphidia* Ponomarenko

†*Baisoraphidia* Ponomarenko, 1993: 73. Type species: †*Baisoraphidia glossopteron* Ponomarenko, 1993, original designation.

†*Baisoraphidia glossopteron* Ponomarenko

†*Baisoraphidia glossopteron* Ponomarenko, 1993: 74. Upper Jurassic–Lower Cretaceous, Baisa, Buryat, Russia.

†*Baisoraphidia orientalis* Ponomarenko

†*Baisoraphidia orientalis* Ponomarenko, 1993: 75. Upper Jurassic–Lower Cretaceous, Baisa, Buryat, Russia.

Genus †*Huaxiaraphidia* Hong

†*Huaxiaraphidia* Hong, 1992a: 101. Type species: †*Huaxiaraphidia sinensis* Hong, 1992a, original designation.

COMMENTS: This genus may be a synonym of *Mesoraphidia*. Examination of the holotypes is required to confirm some of Hong's (1992a) dubious characters. *Huaxiaraphidia shandongensis* Hong does not appear to be congeneric with *H. sinensis* Hong.

†*Huaxiaraphidia shandongensis* Hong

†*Huaxiaraphidia shandongensis* Hong, 1992a: 102. Lower Cretaceous, Beipiao, Liaoning, China.

†*Huaxiaraphidia sinensis* Hong

†*Huaxiaraphidia sinensis* Hong, 1992a: 102. Lower Cretaceous, Beipiao, Liaoning, China.

Genus †*Jilineraphidia* Hong and Chang

†*Jilineraphidia* Hong and Chang, 1989: 291. Type species: †*Jilineraphidia dalaziensis* Hong and Chang, 1989, monobasic and original designation.

†*Jilineraphidia dalaziensis* Hong and Chang

†*Jilineraphidia dalaziensis* Hong and Chang, 1989: 291. Lower Cretaceous, Zhixin, Jilin Province, China.

Genus †*Kezuoraphidia* Willmann

†*Kezuoraphidia* Willmann, 1994: 176. Type species: †*Xuraphidia kezuoensis* Hong, 1992c, monobasic and original designation.

COMMENTS: This genus may eventually prove to be synonymous with *Baisoraphidia*.

†*Kezuoraphidia kezuoensis* (Hong)

†*Xuraphidia kezuoensis* Hong, 1992c: 4. Lower Cretaceous, Kezuo, Liaoning, China.

†*Kezuoraphidia kezuoensis* (Hong), Willmann, 1994: 176.

Genus †*Mesoraphidia* Martynov

†*Mesoraphidia* Martynov, 1925a: 235. Type species: †*Mesoraphidia grandis* Martynov, 1925a, original designation.

†*Phiradia* Willmann, 1994: 178. Type species: †*Mesoraphidia pterostigmalis* Martynov, 1947, monobasic and original designation. TENTATIVE SYNONYMY.

†*Yanoraphidia* Ren in Ren et al., 1995: 98. Type species: †*Yanoraphidia gaoi* Ren in Ren et al., 1995, monobasic and original designation. NEW SYNONYMY.

†*Mioraphidia* Ren, 1997: 178. Type species: †*Mesoraphidia furcivenata* Ren in Ren et al., 1995, monobasic and original designation. NEW SYNONYMY.

†*Xynoraphidia* Ren, 1997: 183. Type species: †*Archeraphidia shangyuanensis* Ren, 1994, original designation. NEW SYNONYMY.

†*Caloraphidia* Ren, 1997: 183. Type species: †*Caloraphidia glossophylla* Ren, 1997, monobasic and original designation. NEW SYNONYMY.

COMMENTS: Several species placed in the family Alloraphidiidae and the genus *Alloraphidia* or allied genera by Ren (1994) and Ren et al. (1995) are obviously misplaced. None of these species exhibit the elongate wings, MA strongly distad origination of MP (in Ren's species MA is only slightly distad MP origination, as in some mesoraphidiid species), the apparent trifurcation of the stems of R, M, and CuA in the forewing (in Ren's species M and CuA are fused for some distance after separating from R), and the short pterostigma that are typical of *Alloraphidia*. As I have already mentioned the distinctions between the Alloraphidiidae and Mesoraphidiidae are weak and the former should perhaps be placed within Mesoraphidiidae. Despite this, none of the Chinese species that I have transferred have synapomorphies that would ally them with *Alloraphidia* even if alloraphidiids were considered a clade of Mesoraphidiidae (at any rank, subfamily or tribe).

†*Mesoraphidia amoena* Ren

†*Mesoraphidia amoena* Ren, 1997: 181. Lower Cretaceous, Beipiao, Liaoning, China.

†*Mesoraphidia elongata* Martynov

†*Mesoraphidia elongata* Martynov, 1925a: 240. Upper Jurassic, Kazakhstan.

†*Mesoraphidia furcivenata* Ren, resurrected combination

†*Mesoraphidia furcivenata* Ren in Ren et al., 1995: 98. Lower Cretaceous, Liaoning, China.

†*Mioraphidia furcivenata* (Ren); Ren, 1997: 179.

†*Mesoraphidia gaoi* (Ren), new combination

†*Yanoraphidia gaoi* Ren in Ren et al., 1995: 99.  
Lower Cretaceous, Liaoning, China.

†*Mesoraphidia glossophylla* (Ren),  
new combination

†*Caloraphidia glossophylla* Ren, 1997: 183.  
Lower Cretaceous, Beipiao, Liaoning, China.

†*Mesoraphidia gobiensis* Ponomarenko

†*Mesoraphidia gobiensis* Ponomarenko, 1988: 73.  
Upper Jurassic, Mongolia.

†*Mesoraphidia grandis* Martynov

†*Mesoraphidia grandis* Martynov, 1925a: 236.  
Upper Jurassic, Kazakhstan.

†*Mesoraphidia heteroneura* Ren

†*Mesoraphidia heteroneura* Ren, 1997: 179.  
Lower Cretaceous, Beipiao, Liaoning, China.

†*Mesoraphidia inaequalis* Martynov

†*Mesoraphidia inaequalis* Martynov, 1925b: 569.  
Upper Jurassic, Kazakhstan.

†*Mesoraphidia longistigmosa* (Ren),  
new combination

†*Alloraphidia longistigmosa* Ren, 1994: 133.  
Lower Cretaceous, Beipiao, Liaoning, China.

†*Mesoraphidia luzzii* Grimaldi

†*Mesoraphidia luzzii* Grimaldi, 2000: 261. Upper  
Cretaceous (Turonian), New Jersey amber.

†*Mesoraphidia myrioneura* (Ren),  
new combination

†*Phiradia myrioneura* Ren, 1997: 178. Lower  
Cretaceous, Beipiao, Liaoning, China.

†*Mesoraphidia obliquivenatica* (Ren),  
new combination

†*Alloraphidia obliquivenatica* Ren, 1994: 134.  
Lower Cretaceous, Beipiao, Liaoning, China.

†*Alloraphidia obligivenata* Hong, 1998: 293.  
*Lapsus calami*.

†*Mesoraphidia parvula* Martynov

†*Mesoraphidia parvula* Martynov, 1925a: 241.  
Upper Jurassic, Kazakhstan.

†*Mesoraphidia polyphlebia* (Ren),  
new combination

†*Archeraphidia polyphlebia* Ren, 1994: 136.  
Lower Cretaceous, Beipiao, Liaoning, China.

†*Xynoraphidia polyphlebia* (Ren); Ren, 1997:  
183.

†*Mesoraphidia pterostigmalis* Martynova,  
resurrected combination

†*Mesoraphidia pterostigmalis* Martynova, 1947:  
635. Upper Jurassic, Kazakhstan.

†*Phiradia pterostigmalis* (Martynova); Willmann,  
1994: 178.

†*Mesoraphidia shangyuanensis* (Ren),  
new combination

†*Archeraphidia shangyuanensis* Ren, 1994: 135.  
Lower Cretaceous, Beipiao, Liaoning, China.

†*Xynoraphidia shangyuanensis* (Ren); Ren, 1997:  
183.

†*Mesoraphidia similis* Martynov

†*Mesoraphidia similis* Martynov, 1925a: 238. Up-  
per Jurassic, Kazakhstan.

†*Mesoraphidia sinica* Ren

†*Mesoraphidia sinica* Ren, 1997: 180. Lower  
Cretaceous, Beipiao, Liaoning, China.

Genus †*Metaraphidia* Whalley

†*Metaraphidia* Whalley, 1985: 147. Type species:  
†*Metaraphidia confusa* Whalley, 1985, mono-  
basic and original designation.

COMMENTS: This is perhaps the most basal ge-  
nus of Mesoraphidiidae, retaining the plesiom-  
orphic separation of A3 and A2 in the forewing  
(fused in other Mesoraphidiidae). This plesiom-  
orphic feature is also present in the Baissopter-  
idae. Willmann (1994) provides a corrected diag-  
nosis for the genus.

†*Metaraphidia confusa* Whalley

†*Metaraphidia confusa* Whalley, 1985: 148. Low-  
er Jurassic (Liassic), England.

†*Metaraphidia vahldieki* Willmann

†*Metaraphidia vahldieki* Willmann, 1994: 174. Lower Jurassic (Liassic), Germany.

Genus †*Nanoraphidia* Engel

†*Nanoraphidia* Engel, herein. Type species: †*Nanoraphidia electroburmica* Engel, herein, monobasic and original designation.

†*Nanoraphidia electroburmica* Engel

†*Nanoraphidia electroburmica* Engel, herein. Upper Cretaceous (Cenomanian) amber, Myanmar.

Genus †*Proraphidia* Martynova

†*Proraphidia* Martynova, 1947: 636. Type species: †*Proraphidia turkestanica* Martynova, 1947, monobasic and original designation.

†*Pararaphidia* Hong, 1992c: 12. *Lapsus calami*.

†*Proraphidia turkestanica* Martynova

†*Proraphidia turkestanica* Martynova, 1947: 636. Upper Jurassic, Karatau, Kazakhstan.

Genus †*Siboptera* Ponomarenko

†*Siboptera* Ponomarenko, 1993: 71. Type species: †*Siboptera eurydictyon* Ponomarenko, 1993, original designation.

†*Liaoraphidia* Ren, 1994: 132. Type species: †*Liaoraphidia fornicata* Ren, 1994, monobasic and original designation.

†*Siboptera* Ren, 1997: 176. *Lapsus calami*.

COMMENTS: *Siboptera* was originally proposed by Ponomarenko (1993) in the family Baissopteridae despite lacking all of the apomorphic characteristics of this family. The genus is weakly distinguished from *Mesoraphidia* and I therefore transfer the genus to the family Mesoraphidiidae.

†*Siboptera eurydictyon* Ponomarenko

†*Siboptera eurydictyon* Ponomarenko, 1993: 71. Upper Jurassic–Lower Cretaceous, Baisa, Buryat, Russia.

†*Siboptera fornicata* (Ren)

†*Liaoraphidia fornicata* Ren, 1994: 133. Lower Cretaceous, Beipiao, Liaoning, China.

†*Siboptera fornicata* (Ren); Ren, 1997: 177.

†*Siboptera medialis* Ponomarenko

†*Siboptera medialis* Ponomarenko, 1993: 73. Upper Jurassic–Lower Cretaceous, Baisa, Buryat, Russia.

Genus †*Sinoraphidia* Hong

†*Sinoraphidia* Hong, 1982: 154. Type species: †*Sinoraphidia viridis* Hong, 1982, monobasic and original designation.

COMMENTS: Hong (1992a, 1992b) presented a revised figure for the venation of *Sinoraphidia* in which the venation was changed not in minor details but dramatically! Owing to the fanciful illustrations frequently provided by this author for various taxa when compared to photographs of the same specimens and his general inability to identify most insects (e.g., Protobanidae described by Hong [1982] as a horsefly is a homopteran! see Grimaldi [1990]), the peculiarities of this genus must be considered dubious at best. From the available evidence this is without doubt a mesoraphidiid, although its position within this family is uncertain.

†*Sinoraphidia viridis* Hong

†*Sinoraphidia viridis* Hong, 1982: 154. Upper Jurassic–Lower Cretaceous, Gansu, China.

Genus †*Xuraphidia* Hong

†*Xuraphidia* Hong, 1992c: 3. Type species: †*Xuraphidia liaoxiensis* Hong, 1992c, original designation.

COMMENTS: This genus is likely a synonym of *Mesoraphidia* or perhaps even *Baisoraphidia*.

†*Xuraphidia liaoxiensis* Hong

†*Xuraphidia liaoxiensis* Hong, 1992c: 4. Lower Cretaceous, Kezuo, Liaoning, China.

†PRISCAENIGMATIDAE, new family

TYPE GENUS: †*Priscaenigma* Whalley, 1985.

DIAGNOSIS: I agree with Willmann (1994) that this group differs fundamentally from all other families of Raphidioptera and is perhaps the adelphotaxon of the remainder of the order. The family retains traits with Megaloptera and also some Neuroptera, particularly in features of the subcosta. In the forewing Sc extends nearly to the wing apex before fusing with R, a condition identical to that state seen in the Megaloptera and some Neuroptera. In all other Raphidioptera Sc meets with C near the wing midpoint and may some-

times bend back to fuse with R as a short cross-vein (frequently just proximad the pterostigma). In the hind wing, however, the typical raphidipteran condition of Sc terminating into C is exhibited (observable in *Hondelagia*). The priscaenigmatids likely share with Baissopteridae the plesiomorphic retention of numerous distal cross-veins, however, the exact homologization of such an attribute requires clarification and is quite problematic. Other features of the family include the simple CuP, the absence of a distinct, ovoid, basal cell between A1 and A2 in the forewing, a narrow costal area, and Rs + M separating from the stem of R together.

Owing to a combination of their presumed phylogenetic position and highly distinctive traits, the priscaenigmatids are here segregated into a separate suborder, the Priscaenigmatomorpha (**new suborder**). The diagnosis of the suborder is identical to that of the family.

#### Genus †*Hondelagia* Bode

†*Hondelagia* Bode, 1953: 269. Type species: †*Hondelagia reticulata* Bode, 1953, monobasic and original designation.

#### †*Hondelagia reticulata* Bode

†*Hondelagia reticulata* Bode, 1953: 269. Lower Jurassic (Liassic), Germany.

†*Mesoraphidia reticulata* (Bode); Oswald, 1990: 162.

COMMENTS: Bode (1953) originally placed this species in Mantispidae but it was subsequently referred to Raphidioptera by Lambkin (1986).

#### Genus †*Priscaenigma* Whalley

†*Priscaenigma* Whalley, 1985: 148. Type species: †*Priscaenigma obtusa* Whalley, 1985, monobasic and original designation.

#### †*Priscaenigma obtusa* Whalley

†*Priscaenigma obtusa* Whalley, 1985: 148. Lower Jurassic (Liassic), England.

#### Family RAPHIDIIDAE Latreille

#### Genus *Ohmella* H. Aspöck and U. Aspöck

#### †“*Ohmella*” *coffini* Nel

†*Ohmella coffini* Nel, 1993: 100. Upper Miocene, Ardèche, France.

#### Genus *Raphidia* Linnaeus

*Raphidia* Linnaeus, 1758: 552. Type species: *Raphidia ophiopsis* Linnaeus, 1758, monobasic.

†*Megaraphidia* Cockerell, 1907: 607. Type species: †*Megaraphidia elegans* Cockerell, 1907, monobasic.

†*Archiraphidia* Handlirsch, 1910: 103. Type species: †*Inocellia tumulata* Scudder, 1890, monobasic.

†*Dictyoraphidia* Handlirsch, 1910: 103. Type species: †*Inocellia veterana* Scudder, 1890, monobasic.

*Raphidia* (*Nigroraphidia*) H. Aspöck and U. Aspöck, 1968a: 58. Type species: *Raphidia palaeiformis* H. Aspöck and U. Aspöck, 1968a, original designation.

*Raphidia* (*Pretzmanna*) H. Aspöck and U. Aspöck, 1968a: 59. Type species: *Raphidia euxina* Navas, 1915b, monobasic and original designation.

*Raphidia* (*Aserbeidshanoraphidia*) H. Aspöck and U. Aspöck, 1968b: 90. Type species: *Raphidia nuchensis* H. Aspöck, U. Aspöck, and Martynova, 1968, monobasic and original designation.

COMMENTS: The genus *Raphidia* as it is currently understood is restricted to the Old World although many of the species listed below are from North America. The North American compression fossils could potentially be placed in *Agulla*, however, in the absence of information from characters other than wing venation such an assignment cannot be made with confidence. Carpenter (1936) believed that the proximal separation of M in the hind wing precluded the compression fossil species from *Agulla*, but in fact this is not the case and the position of the separation of M blends perfectly across the species of *Agulla* and *Raphidia* (see Aspöck et al., 1991). Similarly, the Baltic amber species *Raphidia baltica* Carpenter is perhaps not truly representative of this genus. Until a revision of these fossils can be completed, however, I have conservatively retained them all in *Raphidia* as has been done by past paleoentomologists (e.g., Carpenter, 1936, 1956, 1992; Oswald, 1990) and concomitantly considered the fossil genera *Megaraphidia*, *Archiraphidia*, and *Dictyoraphidia* as tentative junior subjective synonyms of *Raphidia*. Truly these fossils and the associated genus-group names will need to be eventually reassigned within the Raphidiidae.

#### †“*Raphidia*” *baltica* Carpenter

†*Raphidia baltica* Carpenter, 1956: 78. Middle Eocene (Lutetian), Baltic amber.

†“*Raphidia*” *creedei* Carpenter

†*Raphidia creedei* Carpenter, 1936: 150. Oligocene, Creede, Colorado.

†“*Raphidia*” *elegans* (Cockerell)

†*Megaraphidia elegans* Cockerell, 1907: 607. Eocene-Oligocene boundary, Florissant, Colorado.  
†*Raphidia elegans* (Cockerell); Carpenter, 1936: 146.

†“*Raphidia*” *exhumata* Cockerell

†*Raphidia exhumata* Cockerell, 1909: 73. Eocene-Oligocene boundary, Florissant, Colorado.  
†*Raphidia pulveris* Cockerell, 1914: 714. Eocene-Oligocene boundary, Florissant, Colorado.

†“*Raphidia*” *mortua* Rohwer

†*Raphidia mortua* Rohwer, 1909: 533. Eocene-Oligocene boundary, Florissant, Colorado.

†“*Raphidia*” *tranquilla* Scudder

†*Raphidia tranquilla* Scudder, 1890: 154. Eocene-Oligocene boundary, Florissant, Colorado.  
†*Inocellia somnolenta* Scudder, 1890: 157. Eocene-Oligocene boundary, Florissant, Colorado.  
†*Archiraphidia tranquilla* (Scudder); Handlirsch, 1910: 103.

†“*Raphidia*” *tumulata* (Scudder)

†*Inocellia tumulata* Scudder, 1890: 158. Eocene-Oligocene boundary, Florissant, Colorado.  
†*Inocellia eventa* Scudder, 1890: 160. Eocene-Oligocene boundary, Florissant, Colorado.  
†*Archiraphidia tumulata* (Scudder); Handlirsch, 1910: 103.

†*Archiraphidia eventa* (Scudder); Handlirsch, 1910: 103.

†*Raphidia tumulata* (Scudder); Carpenter, 1936: 149.

†“*Raphidia*” *veterana* (Scudder)

†*Inocellia veterana* Scudder, 1890: 156. Eocene-Oligocene boundary, Florissant, Colorado.  
†*Dictyoraphidia veterana* (Scudder); Handlirsch, 1910: 104.  
†*Raphidia veterana* (Scudder); Carpenter, 1936: 145.

#### INCERTAE SEDIS

Genus †*Archiinocellia* Handlirsch

†*Archiinocellia* Handlirsch, 1910: 100. Type species: †*Archiinocellia oligoneura* Handlirsch, 1910, monobasic.

†*Archiinocellia oligoneura* Handlirsch

†*Archiinocellia oligoneura* Handlirsch, 1910: 100. Oligocene, British Columbia, Canada.

†*Arariperaphidia*

Martins-Neto and Vulcano

†*Arariperaphidia* Martins-Neto and Vulcano, 1989: 243. Type species: †*Arariperaphidia rochai* Martins-Neto and Vulcano, 1989, monobasic and original designation.

†*Arariperaphidia rochai*

Martins-Neto and Vulcano

†*Arariperaphidia rochai* Martins-Neto and Vulcano, 1989: 245. Lower Cretaceous, Ceará, Brazil.



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